INFORMATION TRANSFER THROUGH INTRASPECIFIC INTERACTIONS IN A LYCOSID SPIDER

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Information transfer through intraspecific interactions in a lycosid spider.– The transfer of information during agonistic and sexual interactions between adults of *Lycosa tarentula fasciiventris* is studied. Information theory and correspondence analysis are applied to the intra-individual transition matrices. Information is quantitatively similar regardless of the context and the sex. Similarity arises mainly from the transition between motionless and approaching-signalling patterns. There are no patterns strongly predicting the immediate retreat of the sender and there is a marked predictability of females immediately attacking in their agonistic interactions. Results fit those expected if risk of intraspecific interactions in such a solitary predator was among the selective pressures leading to the evolution of communication systems.

Key words: Spiders, Lycosidae, Animal communication, Information theory, Correspondence analysis.

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INTRODUCTION

Spiders are mainly solitary predators, and their feeding pattern is among the main factors that influence spider behaviour (Christenson, 1984a, 1984b). This factor is usually thought to lead to spider intraspecific interactions being risky, so intraspecific communication is considered to be important among this group (Krafft, 1982; Witt, 1982). To the extent that these risks are to be similar, quantitative differences are not expected if one compares the information transfer in the agonistic and the sexual interactions in a single species. Predictability of behaviour is expected to be high in the two types of contexts (Fentress, 1981). Qualitative differences may appear to the extent that these two kinds of interactions differ functionally.

Lycosa tarentula fasciiventris (Lycosidae) is a solitary burrowing wolf-spider, living on the Iberian peninsula. Animals reach their adult stage in the late spring of their second year of life, and adult males wander in search of females as in most spider species (SCHMITT et al., 1990; WATSON, 1990). Male survival in the field is limited to some weeks after moulting, whereas adult females can survive for more than two years in the laboratory. Adult females continue to occupy their burrows. Under laboratory conditions, agonistic and sexual interactions between adult individuals of this species seem to involve some kind of communicative process (FERNÁNDEZ-MONTRAVETA & ORTEGA, 1990a, 1991; ORTEGA et al., 1984, 1986). In this paper, the significance of this communicative process by means of information theory and correspondence analysis is analyzed. Agonistic and sexual interactions are compared to test whether the information transferred is quantitatively similar, regardless of differences in these two types of interactions (i.e. aggressive or sexual).

MATERIAL AND METHODS

In this study 86 adult males and 75 adult females were used. Animals were captured

Table 1. Behavioural patterns shown by males (M) and females (F) during the agonistic (AG) and the sexual (SX) interactions, with a brief description of some of the patterns. For a broader description see ORTEGA et al. (1984, 1986) and FERNÁNDEZ-MONTRAVETA & ORTEGA (1990a).

Pattern	Sex	Context	Description
Motionless (M)	♂	AG, SX	Resting or raising body, legs on the substrate
	♀	AG, SX	
Extended foreleg (EF)	♂	AG	Raised foreleg aligned to the body
		SX	Raising angle up to 90° C
Approach (AP)	♂	SX	
	♀	AG, SX	
Approach with waving foreleg (AW)	♂	AG, SX	Approach while forelegs are raised and lowered in a slow and alternating way
Approach with extended foreleg (AE)	♂	AG, SX	Approaching while forelegs remain raised as in EF
Pounce (PC)	♀	AG, SX	One female jumping towards the other spider, foreleg being extended and chelicerae spread out
Go away (GW)	♂, ♀	AG, SX	
Foreleg contact (CT)	♂	AG	
	♀	AG, SX	
Foreleg on female body (CB)	♂	SX	
Mount (MT)	♂	SX	Dorsally passing over the female body
Copulation position (CP)	♀	SX	Female prosoma resting on the substrate, opistosoma raised and laterally turned
Palpal drumming (DM)	♂	AG	Short bursts of palp vibrating and alternatively taping on the substrate
	♀	AG, SX	Brief and less intense series of palp vibration
	♂	SX	Longer and more irregular series of palps vibrating and scratching on the substrate
Fight (FG)	♂	AG	Males repeatedly rushing at one another
Tangle (TG)	♀	AG, SX	All legs interlaced
Capture (CR)	♀	AG	
Extended foreleg and chelicеae spread out (ECh)	♀	AG, SX	Forelegs raised, chelicerae fangs opened

at Cantoblanco (Madrid) in their penultimate developmental stage and afterwards were kept isolated, under controlled photoperiod (artificial daylight, 10h light:14h darkness) and temperature (25 ± 5° C) conditions. Blow-flies were supplied as prey twice weekly.

Adult individuals were observed in randomly assigned pairs. Two types of pairs were observed: those involving individuals of the same sex (agonistic encounters) and those involving individuals of the opposite sex (sexual encounters). Male-male and male-female pairs were observed in summer, whereas female-female pairs were observed in spring after their moulting to adult stage. Sixty different male pairs, 73 female pairs and 131 male-female pairs were observed in all.

Observations were carried out in 30x15x15cm glass terraria with a soil substrate. The burrow was bisected by one glass wall of the terrarium so we were able to see inside it during the observation period. One of the members of the pair was transferred to the observation terrarium immediately before the observation began. At that time the other member of the pair had already been occupying the terrarium for at least one week. Males were always transferred to the terrarium previously occupied by females.

Observations lasted no less than 30 min. If an interaction took place, observation was prolonged until the interaction finished. When the two animals were outside the burrow, we considered that an interaction began when animals were closer than 5 cm and one of them was oriented towards the other (ASPEY, 1977). If one of the members of the pair was inside the burrow, interaction was considered to begin when the other animal put its forelegs on the upper edge of the burrow. From records of the behaviour shown by each animal during the interaction, the intra-individual behaviour sequence was scored. Table 1 summarizes the patterns of behaviour we noted, with regards both to the context and to the sex.

All the feasible two-act transitions were extracted from the intra-individual sequences of behaviour. Transition matrices were constructed in which the frequency with which one pattern (preceding act) was immediately followed by each of the other ones (subsequent act) was recorded. Auto-transitions were considered not to occur. In the case of female agonistic interactions, capture was considered to occur only as a subsequent act, whereas copulation position was considered to occur only as subsequent act in female sexual sequences.

Information theory was applied to these transition matrices. Normalized transmission of information (t) was calculated as an index of the information transfer (T) with regards to the behavioural diversity (H), usually considered as an index of the information content (STEINBERG, 1977; STEINBERG & CONNANT, 1974).

$$t = \frac{T\,(X, Y)}{H\,(Y)}$$

$$T\,(X, Y) = H\,(Y) + H\,(X) - H\,(X, Y)$$

$$H(X, Y) = \frac{1}{N}\,(N \log_2 N - \Sigma n_{ij} \log_2 n_{ij})$$

$$H\,(Y) = \frac{1}{N}\,(N \log_2 N - \Sigma n_j \log_2 n_j)$$

$$H\,(X) = \frac{1}{N}\,(N \log_2 N - \Sigma n_i \log_2 n_i)$$

N being the total number of two-act transitions; n_{ij} the observed frequency of pattern i being followed by pattern j; n_i, n_j being, respectively, the observed frequencies of patterns i and j.

T' was calculated from T,

$$T' = T - \frac{(r-1)\ (c-1)}{1.3863\ N}$$

r being the number of rows and c the number of columns.

The same transition matrices were analyzed by means of correspondence analysis (SENAR, 1989; HEIJDEN VAN DER et al., 1990). To that end, the PRINCOMP.EXE program (Dr. J. Podari, Research Inst. for Ecology and Botany, Hungarian Academy of Sciencies) was applied. We determined the percentage of the total variance (% Total V) and that of the common variance (% Common V) explained by each of the axis. We also determined the coordinates of each pattern on each axis and the contribution of the patterns to the variance of the axes (absolute contribution AC). The relative contribution (RC), defined as the squared correlation between each pattern and each of the axes was also calculated.

RESULTS

A total number of 1335 transitions between patterns of male agonistic behaviour, 1439 transitions in the case of female agonistic behaviour, 3933 transitions between patterns of male sexual behaviour and 967 transitions in the case of female sexual behaviour were analyzed. Results from applying information theory to these matrices are summarized in table 2. T differs from zero in all the cases. T values are quite similar if compared either between contexts or between sexes, being greater for the male behaviour than for the female behaviour, regardless of the context. Neither does T' show any noticeable difference when sexual and agonistic contexts are compared within each sex. If "t" values are compared with regard to either sex or context, an even stronger resemblance becomes apparent. Information transferred accounts for up to 38% of the behavioural diversity. As for H(X) and H(Y), they do neither differ if compared either between contexts or between sexes. Sex-differences are greater than context-differences (table 2).

Table 2. Information content (H) and uncertainty reduction (T, T', t) during intraspecific interactions with regards to the context (agonistic and sexual) and the sex.

	Agonistic		Sexual	
	♂	♀	♂	♀
H (X)	2.68	2.54	2.61	2.49
H (Y)	2.72	2.62	2.69	2.60
T (X, Y)	1.05	0.94	0.99	0.94
T' (X, Y)	1.02	0.91	0.98	0.89
t	0.38	0.35	0.36	0.34

Correspondence analysis shows that the similarity between the two types of interactions mainly comes from patterns of motionless and moving alternating in a single axis. Thus, from the seven axes the program identified in all, the first three axes account for 89.1% (male agonistic behaviour), 88.7% (female agonistic behaviour), 89% (male sexual behaviour) and 95% (female sexual behaviour) of the total variance. In turn, the most of the common variance of the axes is accounted for by the first axis (51.4%, 59.3%, 65.2% and 65.2% for male and female agonistic and sexual behaviour, respectively). In all the cases, the first axis variability is mostly explained by the pattern "Motionless" (M), both as the preceding and as the subsequent act (tables 3-6).

In male agonistic sequences, three other patterns ("Go away" GW, "Approach with waving forelegs" AW, and "Drumming"

DM) also contribute to this axis variability, the four patterns together explaining up to 92.62% of the axis variability as preceding acts. A less marked contribution to this axis determination is made by these three patterns as subsequent acts. Taken together with Motionless, they account for 94.3% of the axis variability. The second axis is mainly accounted for by "Foreleg contact" (CT) as the preceding act, "Extended foreleg" (EF) contributing to the axis variability to a lesser extent, with "Fight" (FG) being the pattern which mainly explains the axis as the subsequent act. The third axis is mainly determined by "Approach with extended foreleg" (AE) as the preceding act. As for the subsequent acts, "Foreleg contact" and, to a lesser extent "Approach with waving forelegs" are the patterns which mainly account for this axis variability (table 3). Three different factors then arise which mainly explain the male agonistic behaviour: careful approaching (alternating moving and motionless patterns), contact and signalling, where "Approach with extended foreleg" and "Foreleg contact" are associated. Plotted against the first and the third factorial axes, a sequential relationship appears between "Motionless" and "Approach with waving foreleg", "Drumming" and "Go away", as well as between "Approach with extended forelegs" and "Foreleg contact" (fig. 1).

In female agonistic sequences, the first factorial axis variability is also explained by "Motionless", "Approach" (AP) and "Go away", both as preceding (90.36%) and as subsequent acts (91.98%). The second factorial axis is mostly determined by "Pounce" (PC) and "Foreleg contact" (75.49%) as preceding patterns, "Extended foreleg and chelicerae spread out" (ECh), "Tangle" (TG) and "Foreleg contact" explaining the axis as subsequent patterns (72.13%). As for the third factorial axis, it is mainly determined by "Extended foreleg and chelicerae spread out", "Foreleg contact" and "Tangle" as preceding acts (83.07%) and "Foreleg contact", "Extended foreleg and chelicerae spread out", "Drumming" and "Go away" as subsequent acts (83.32%) (table 4). Carefully approaching, attacking and threating appear to be the factors explaining the female agonistic behaviour. Plotted against the first and the second factorial axes, some marked sequential relationships appear. Pounce is likely to be followed by either tangling or capturing, whereas motionless sequentially alternate with approaching and going away, in much the same way than in male agonistic behaviour (fig. 2).

Determination of the axes in male sexual behaviour (table 5) is similar to that obtained for the male agonistic behaviour, except for the stronger contribution of "Drumming" to the first axis, both as the preceding and as the subsequent act in male sexual sequences. "Extended foreleg" is the pattern explaining most of the second factorial axis variability as the preceding act. "Approach with extended foreleg" has the strongest contribution to the axis as subsequent act. As for the main contribution to the variability of the third axis, it is made by "Foreleg on female body" (CB) as the preceding act, while "Mount" is the pattern accounting for most variability as the subsequent act (table 5). Careful approaching, signalling and mounting are then the three main factors in explaining the male sexual behaviour. Plotted against the first and second factorial axes, a marked sequential relationship appears between "Extended foreleg" and "Approach with extended foreleg", as well as between "Motionless" and "Approach", "Approach with waving foreleg" and "Go away" (fig. 3).

For female sexual behaviour (table 6),

Table 3. Male agonistic sequences: absolute contribution (AC) and relative contribution (RC) of each of the axes on the behavioural patterns as preceding (capital letters) and as subsequent acts (small letters); V. Variance. (See table 1 for abbreviations).

	Axis					
	AX 1		AX 2		AX 3	
Pattern	AC	RC	AC	RC	AC	RC
Preceding						
M	34.45	79.90	1.18	1.50	18.04	16.30
EF	4.71	17.70	17.10	34.90	15.62	22.70
AE	0.72	2.70	2.37	4.80	50.84	73.20
AW	15.76	89.50	0.57	1.80	0.30	0.70
GW	27.23	89.10	0.13	0.20	6.13	7.80
CT	1.69	3.60	76.26	88.40	7.04	5.80
FG	0.25	4.70	1.36	14.10	0.72	5.30
DM	15.18	78.20	0.53	1.50	1.16	2.30
Subsequent						
m	58.04	95.40	0.28	0.30	5.42	3.50
ef	0.16	1.30	6.16	28.50	2.61	8.60
ae	4.84	37.10	4.45	18.60	1.20	3.60
aw	10.62	59.60	1.48	4.50	11.30	24.50
gw	13.00	61.30	5.84	15.00	5.40	9.90
ct	0.01	0.00	11.03	18.60	65.10	78.30
fg	0.75	1.80	62.05	83.30	8.02	7.70
dm	12.62	67.20	7.56	21.90	0.92	1.90
% Com. V	51.45		28.26		20.00	
% Total V	46.06		25.10		17.90	

Table 4. Female agonistic sequences: absolute contribution (AC) and relative contribution (RC) of each of the axes on the behavioural patterns as preceding (capital letters) and as subsequent acts (small letters); V. Variance. (See table 1 for abbreviations).

	Axis					
	AX 1		AX 2		AX 3	
Pattern	AC	RC	AC	RC	AC	RC
Preceding						
M	46.24	89.80	10.36	9.10	0.04	0.00
AP	22.18	88.10	0.92	1.70	5.38	4.80
GW	21.94	85.30	5.69	10.00	3.09	2.70
CT	1.04	5.50	17.88	43.30	25.04	29.90
PC	0.15	0.50	57.61	88.00	4.83	3.60
DM	6.79	77.00	0.26	1.30	3.46	8.80
ECh	1.01	6.90	3.18	9.90	37.55	57.40
TG	0.70	4.70	3.84	11.80	20.48	31.10
Subsequent						
m	52.48	91.40	10.56	8.30	0.53	0.20
ap	17.00	75.40	9.43	18.90	0.46	0.50
gw	22.50	87.10	0.27	0.50	10.97	9.50
ct	0.73	4.00	17.87	44.90	34.52	42.80
pc	0.34	64.30	1.10	6.00	4.67	12.50
dm	6.46	1.50	1.57	7.10	11.16	24.80
ech	0.32	0.10	29.37	63.40	26.67	28.40
cr	0.01	0.10	5.10	17.10	7.70	12.80
tg	0.02	0.10	24.89	90.10	3.40	6.10
% Com. V	59.32		27.12		13.56	
% Total V	52.90		24.00		11.80	

"Motionless" and "Go away" mainly account for the first axis variability as preceding acts (73.95%), "Motionless", "Go away" and "Approach" being those patterns which mainly determine this axis as subsequent acts (87.50%). The second axis is mainly determined by "Pounce" and "Foreleg contact" as preceding acts (70.89%), as in female agonistic behaviour, but "Extended foreleg with chelicerae spread out" is the pattern explaining most of the axis variability as the subsequent act. As for the third factorial axis, it is mainly determined by "Extended foreleg with chelicerae spread out" as the preceding act, whereas "Drumming" and "Foreleg contact" account for most of the variability as subsequent acts (60.05%) (table 6). Carefully approaching and threating are the two main factors explaining the female sexual behaviour. There is noticeable the lack of clear sequential relationship between "Copulation position" and all the other behavioural patterns. Noticeable as well is the sequential relationship between "Extended foreleg with chelicerae spread out" and "Foreleg contact" if plotted against the first-third factorial axes plane (fig. 4).

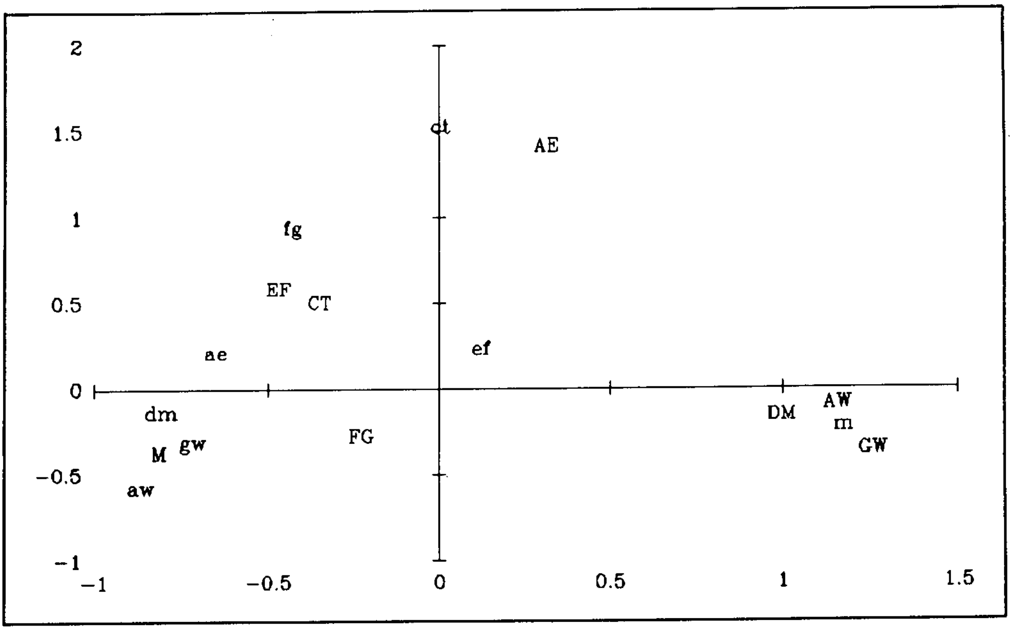

Fig. 1. Plot of male agonistic pattern coordinates on two of the retained factorial axes. The first factorial axis appears in abscises and the third one in ordinates. Preceding acts are represented by capital letters and small letters are used for consequent acts. (See table 1 for abbreviations).

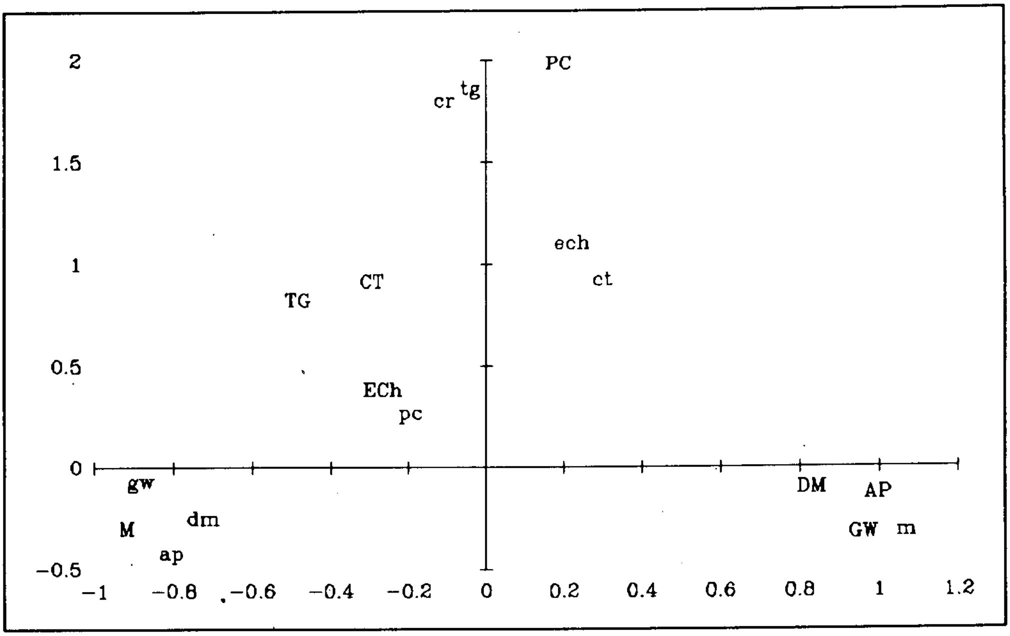

Fig. 2. Plot of female agonistic pattern coordinates on two of the retained factorial axes. The first factorial axis appears in abscises and the second one in ordinates. Preceding acts are represented by capital letters and small letters are used for subsequent acts. (See table 1 for abbreviations).

Table 5. Absolute contribution (AC) and relative contribution (RC) of each of the axes on the behavioural patterns as preceding (capital letters) and as subsequent acts (small letters) in male sexual sequences. V. Variance. (See table 1 for abbreviations).

	Axis					
	AX 1		AX 2		AX 3	
Pattern	AC	RC	AC	RC	AC	RC
Preceding						
M	37.20	83.30	18.70	13.80	5.90	2.60
AP	9.30	79.80	0.20	0.60	3.50	6.00
GW	13.80	93.10	0.10	0.20	1.10	1.50
EF	9.90	28.80	74.20	70.50	0.80	0.40
AE	3.70	27.20	0.00	0.00	29.00	42.90
AW	6.00	72.00	0.20	0.80	2.60	6.20
DM	19.20	79.70	1.20	1.60	0.20	0.20
CB	0.40	3.10	2.50	6.00	47.80	69.80
MT	0.50	8.30	2.90	14.80	9.00	28.40
Subsequent						
m	48.00	95.90	0.40	0.30	4.19	1.70
ap	8.81	58.60	12.89	28.20	7.35	9.70
gw	9.42	48.00	13.23	22.20	13.94	14.20
ef	3.23	26.00	6.21	16.50	3.75	6.00
ae	4.63	19.90	55.08	77.30	0.12	0.10
aw	4.80	63.10	5.25	22.70	4.29	11.20
dm	20.91	87.80	5.78	8.00	3.80	3.20
cb	0.21	2.40	0.89	3.40	15.80	37.80
mt	0.00	0.00	0.28	0.80	46.80	82.20
% Com. V	65.18		21.43		13.39	
% Total V	58.30		19.15		11.60	

Table 6. Absolute contribution (AC) and relative contribution (RC) of each of the axes on the behavioural patterns as preceding (capital letters) and as subsequent acts (small letters) in female sexual sequences. V. Variance. (See table 1 for abbreviations).

	Axis					
	AX 1		AX 2		AX 3	
Pattern	AC	RC	AC	RC	AC	RC
Preceding						
M	50.18	96.60	1.70	1.30	6.04	1.80
AP	12.53	90.60	2.29	6.30	0.39	0.50
GW	23.77	76.20	17.19	21.20	3.06	1.50
PC	0.85	4.10	40.33	75.30	11.48	8.80
ECh	0.24	1.90	2.23	6.80	66.45	83.10
DM	12.25	75.10	4.97	11.70	7.22	7.00
CT	0.14	0.90	30.56	77.80	5.47	5.70
TG	0.10	14.20	0.40	21.70	0.00	0.00
Subsequent						
m	47.03	89.30	14.41	10.50	0.68	0.20
ap	22.00	86.50	2.47	3.70	9.95	6.20
gw	18.47	91.10	0.07	0.10	10.18	7.90
pc	1.56	34.30	0.11	1.00	9.69	33.60
ech	2.65	9.00	66.83	87.00	4.99	2.70
dm	7.75	54.90	2.50	6.80	25.98	29.10
ct	0.14	1.40	6.03	21.70	34.07	50.40
cp	0.32	30.50	0.03	1.20	1.82	27.20
tg	0.03	0.70	7.32	72.60	2.31	9.40
% Com. V	65.18		25.00		9.82	
% Total V	61.60		23.70		9.70	

DISCUSSION

Since T apparently differs from zero, we consider that some information is being transferred during all the intraspecific interactions analyzed here (HALLIDAY, 1983). Information transfer, reflecting a communicative process, thus occurs in both the sexual and the agonistic interactions. Normalized transmission (t), a more suitable index for assessing communicative processes (STEINBERG & CONNANT, 1974), seem to differ even to a lesser extent. We think that these results fit our hypothesis that intraspecific communication is quantitatively similar in the two types of interactions compared here.

Information measured is, on the average, greater than that measured in other arthropod species (DINGLE, 1969; HAZLETT & BOSSERT, 1965; HYATT & SALMON, 1979; STEINBERG & CONNANT, 1974). This result is also consistent with the idea that communication should be important among spiders. However, this statement cannot be generalized, as there are no available data

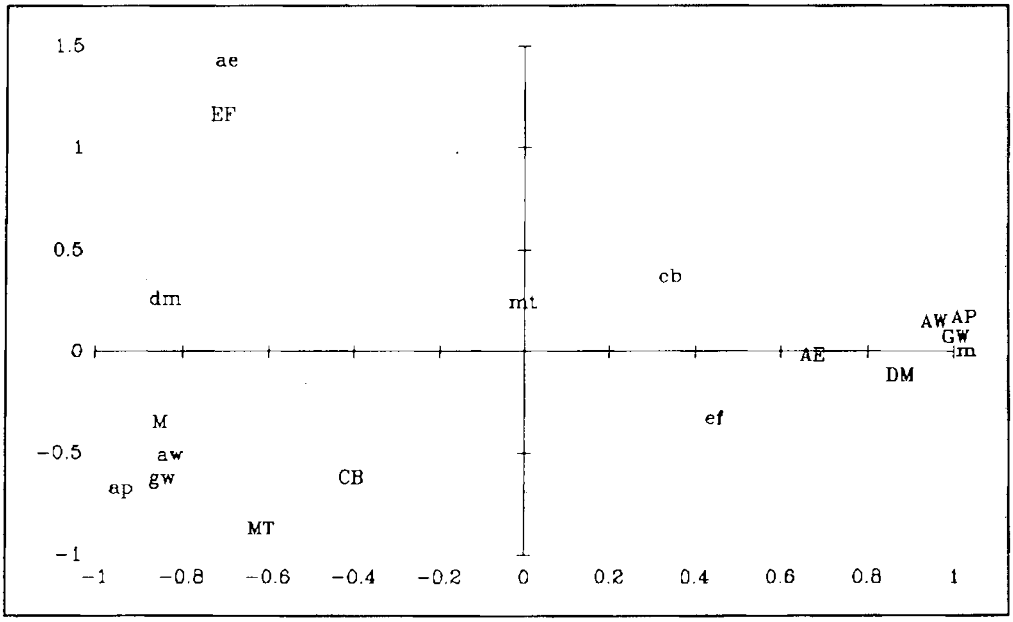

Fig. 3. Plot of male sexual pattern coordinates on two factorial axes. The first factorial axis appears in abscises and the second one in ordinates. Capital letters are for the preceding acts and small letters are used to represent the subsequent acts. (See table 1 for abbreviations).

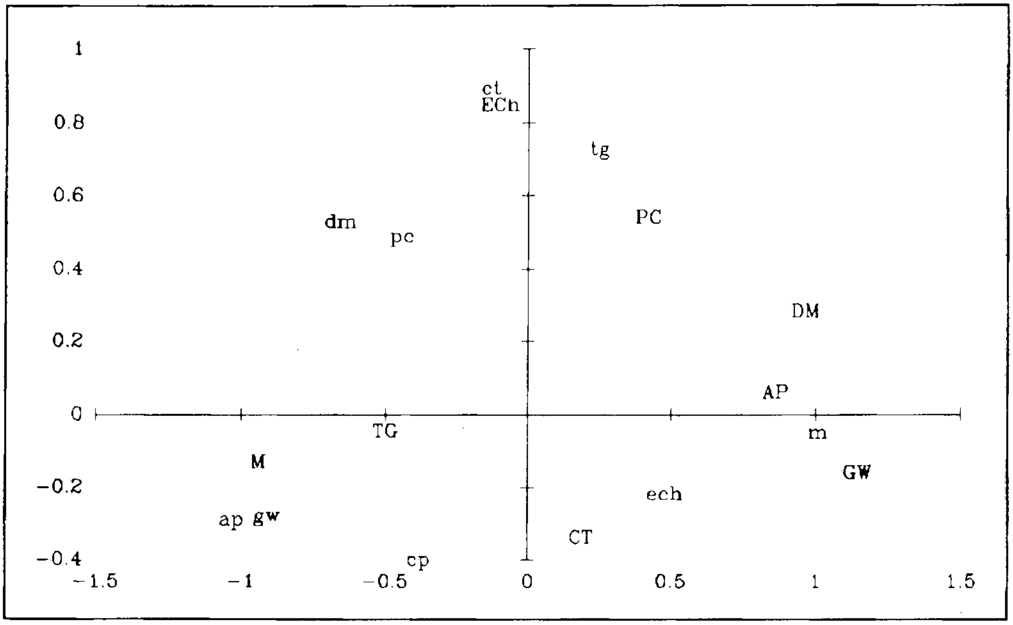

Fig. 4. Plot of female sexual pattern coordinates on two factorial axes. The first factorial axis appears in abscises and the third one in ordinates. Capital letters are for the preceding acts and small letters are used to represent the subsequent acts. (See table 1 for abbreviations).

from other spider species. Comparative analysis is also restricted by the lack of definite criteria which enable the statistical significance of the differences to be assessed, as some of the tests proposed to do it are only useful to the extent that T differs slightly from zero (Fagen in STEINBERG, 1977). These statistical problems have led some researchers to consider information theory as a less useful tool for carrying out interspecific comparisons than previously thought (LOSEY, 1978), though theory is a useful tool in order to compare different intraspecific contexts in a single species (BAYLIS, 1976; DINGLE, 1969).

As for the sources of predictability through the intraindividual sequences, it seems to be mostly related to a single factorial axis loaded most heavily on behaviors associated with transition from motionless to approach. Thus, resemblance between the agonistic and the sexual interactions could mainly arise from animals approaching to each other in a careful way. This interpretation is consistent with our hypothesis that the risk of intraspecific interactions in such a solitary predator is among the main factors shaping the interaction strategies shown by this spider species.

For females, the two other factorial axes are strongly associated with attack and threat. Some female agonistic behaviours, like "Pounce", are likely to be followed by attack ("Tangle" or even "Capture") and are never followed by retreat (see fig. 2). Such a sequential relationship pointing to the immediate attack by the sender is not observed in male agonistic behaviour. Male second and third axes load with behaviours associated with contact. This difference is in agreement with the higher escalation level of female agonistic behaviour. In fact, such an accurate predictability of immediate attack is theoretically expected whenever escalation risks are high (PARKER, 1974), animals not being expected to accurately signal their likelihood of immediately retreating (CARYL, 1979).

As for female sexual behaviour, there is no pattern strongly predicting the immediate receptivity by the female. Instead, predictability is mainly related to threating, as reflected by the relationship between "Extended foreleg and chelicerae spread out" and "Foreleg contact". This transition could inform about the lack of immediate receptivity by females, but it does not seem to lead males to stop courting. Thus, males continue to court females regardless of their being not eventually receptive (FERNÁNDEZ-MONTRAVETA & ORTEGA, 1990b). This fact can be easily understood in terms of the reproductive benefits females obtain from their behaviour. By not giving accurate information about their lack of receptivity, females assure that males will continue to court, female choice being one of the proposed functions for multiple mating in spiders (WATSON, 1991). This interpretation leads us to suggest that females could use male courtship to get information about male characteristics. This assumption should be tested.

We think that predictability of female behaviour is mainly related to the lack of readiness by females to immediately leave or to copulate. As for males, predictability is consistent with the fact that they approach to conspecifics in a careful way. Carefully approaching could allow animals to avoid the predatory response by preventing conspecifics from detecting them at distance. If this is true, the sender would not only actively identify itself as it approaches, but also avoid to release a predatory reaction by the receiver.

Both visual and vibratory signals could be involved in this process. Thus, drumming, waving and raising the forelegs, and chelicerae spreading could be considered as communicative signals. Palpal drumming could probably be a vibratory signal, as in other spider species (HARRISON, 1969; ROVNER, 1967; see BARTH, 1985 for a review) where vibrations play a significant role in the intraspecific communication systems (ROVNER 1975; STRATTON & UETZ, 1981, 1983). The extent to which male and female drumming differ, as reflected by their different contribution to approaching and to threating shown here, should be tested.

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